CYTOTAXONOMIC NOTES ON SOME GENTIANACEAE

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CHROMOSOME NUMBERS HAVE PROVED to be of considerable value in generic delimitation in the Gentianaceae, particularly with regard to *Gentiana* L., *Gentianella* Moench, and their relatives. But of the approximately 65 variously recognized genera, chromosome counts have been previously available for only 33, and of these 11 are monotypic or are known cytologically from only a single count. Chromosome numbers are reported here for 21 species in 11 genera, including 4 genera for which counts have previously been unavailable; one of the counts is tentative, however.

The standard squash technique has been used. Flower buds were fixed in 3:1 ethanol-acetic acid, stored in 70% ethanol, and the pollen-mother-cells were subsequently squashed in acetocarmine. Permanent slides were made using the quick-freeze method of Conger and Fairchild (1953). Voucher specimens are deposited in the herbaria of the Arnold Arboretum (A and AAH), except for that for *Bartonia verna*, which is at DUKE. A summary of the results is presented in TABLE 1; for the sake of comparison, all previously reported counts for the genera investigated are listed in the APPENDIX. Photographs of chromosomes of representatives of each of the genera are shown in FIGURE 1. All photographs were made from temporary slides.

Bartonia Muhl. ex Willd.

The three to four species of *Bartonia*, a genus of semisaprophytes or semiparasites, are distributed in the eastern and central United States and the maritime provinces of Canada. Previously, chromosome numbers were reported for *B. paniculata* (Michx.) Muhl. and *B. virginica* (L.) BSP., both $n = 26$. The chromosome number of *B. verna* (Michx.) Muhl., $n = 22$, is reported here for the first time. Only *B. texana* Correll remains to be investigated cytologically. However, this plant, known from a single locality in Texas, may not be distinct from the variable *B. paniculata*.

Two basic chromosome numbers ($x = 11$ and $x = 13$), which correspond to two morphological groups, are found in this small genus. *Bartonia verna*, restricted to the Coastal Plain of the southeastern United States, is spring-flowering and has relatively long, single-veined corolla lobes. The more widely distributed *B. paniculata* and *B. virginica* are summer-flowering and have short, 3-veined corolla lobes.

Calolisianthus (Griseb.) Gilg

A genus of perhaps ten species, primarily Brazilian in distribution, *Calolisianthus* is unknown cytologically except for the single species reported

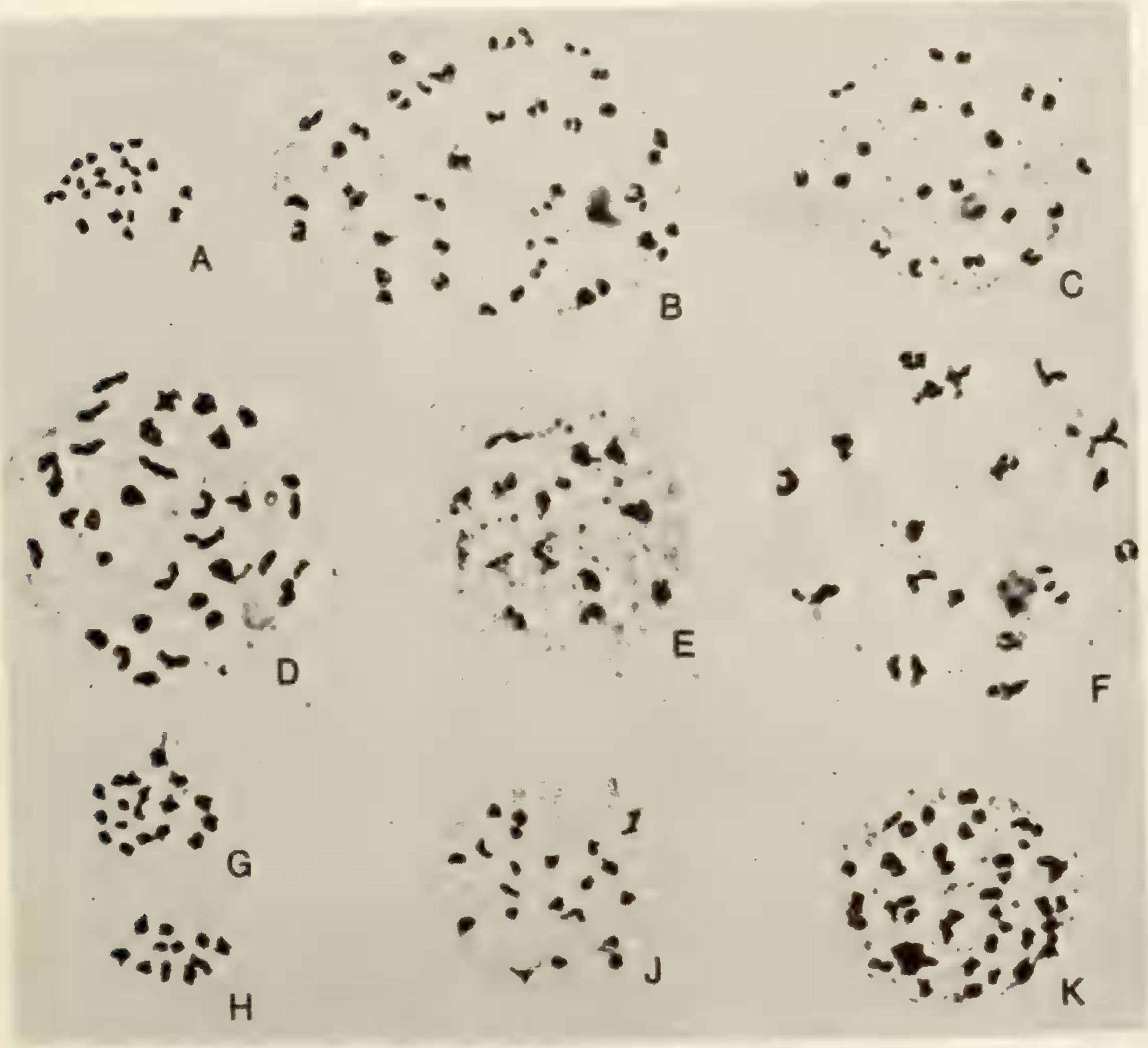

FIGURE 1. Chromosomes of Gentianaceae, × 750: A, *Bartonia verna*, Metaphase II, $n = 22$; B, *Calolisianthus frigidus*, Diakinesis, $n = 40$; C, *Chelonanthus bifidus*, Diakinesis, $n = 20$; D, *Chironia baccifera*, Diakinesis, $n = 34$; E, *Coutoubea spicata*, Diakinesis, $n = 15$; F, *Gentiana sedifolia*, Diakinesis, $n = 20$; G, *Gentianella dacrydioides*, Metaphase II, $n = 18$; H, *Halenia inaequalis*, Metaphase II, $n = 11$; J, *Macrocarpaea glabra*, Diakinesis, $n = 21$; K, *Symbolanthus tricolor*, Diakinesis, $n = 40$.

here. Although *C. frigidus* (Sw.) Gilg does not deviate strikingly from other species in the genus in terms of its floral and vegetative features, Nilsson (1970) found that its pollen more closely resembles that of species of *Symbolanthus* than that of its supposed congeners. The chromosome number of *C. frigidus*, $n = 40$, is the same as that of the two *Symbolanthus* species investigated so far. However, until more is known of the chromosome numbers in both genera, we prefer not to draw any conclusions concerning the relationship of *C. frigidus* to *Symbolanthus*. It certainly would not appear to fit morphologically into that genus.

Chelonanthus (Griseb.) Gilg

The 15 to 20 species of *Chelonanthus* are distributed through much of mainland tropical America. Previously, a chromosome number, $n = 20$, was reported only for *C. alatus* (Aubl.) Pulle (Weaver, 1969). The two

species investigated in this study also have this same number of chromosomes. Although these three species comprise one-fifth or less of the total number of species in the genus, they represent the primary morphological groups: *C. alatus*, with a gibbous-campanulate corolla, a dichasium with long, secund, racemelike side branches, and pollen in tetrads; *C. bifidus* (HBK.) Gilg, with a funnelform corolla, a normal compound dichasium, and pollen in tetrads; and *C. uliginosus* (Griseb.) Gilg, with pollen in polyads. Therefore it is to be expected that $n = 20$ is general in the genus.

Chironia L.

Most of the species of *Chironia*, of which there are around 35, are South African in distribution, but several range northward into tropical Africa and Madagascar. This genus and the very closely related monotypic *Orphium* E. Mey. comprise Gilg's Gentianeae-Chironiinae, delimited primarily on the basis of the large pollen grains of the plants. The chromosome number of *C. baccifera* L. ($n = 34$), reported here for the first time, is the only published one for the genus. Chromosome numbers based on $x = 17$ are rare in the family, having been found elsewhere up to now in only three species of *Sabatia* Adans. (Perry, 1971) and one of *Canscora* Lam. (Mukherjee, 1968).

Chironia baccifera, restricted to South Africa, is the only species in the genus with a berrylike fruit, and it has been considered to constitute a monotypic subgenus.

Coutoubea Aubl.

The three to five species of *Coutoubea* are restricted in distribution to northern South America, with the exception of *C. spicata* Aubl., which ranges north in Central America to British Honduras. The chromosome number $n = 15$, reported here for *C. spicata*, represents the first published count for the genus.

Gentiana L.

A large genus, primarily of the Northern Hemisphere, *Gentiana* in the strict sense has been subdivided into ten sections of greatly varying size. The only species investigated in this study, *G. sedifolia* HBK., belongs to the section CHONDROPHYLLAE Bunge, a group of species low in stature with ± hyaline-margined leaves, usually solitary flowers, symmetrical corolla plaits which are often nearly as large as the corolla lobes, distinct anthers and stigmas, often long-stipitate capsules, and wingless seeds. Most of the species are high-elevation plants, and they are particularly diverse in the Himalayas and the mountains of China. Members of this section are the only species of *Gentiana* found in the Southern Hemisphere. Previously, chromosome numbers have been reported for eleven species in this section, the base numbers being $x = 5$ (seven species), $x = 9$ (one species), and $x = 13$ (three species). All of these base numbers are

present in other sections of *Gentiana*, $x = 13$ being perhaps the commonest and most widespread one in the genus. However, $x = 5$ is common only in sect. GENTIANA and $x = 9$ in sect. MEGALANTHE Gaudin (= sect. THYLACITES Griseb.).

The section CHONDROPHYLLAE contains both annual (or monocarpic) and perennial species, and several authors have subdivided the section into series along these lines. All of the perennial species for which chromosome numbers are available are $n = 13$, while all of the annuals are $n = 10$ or $n = 20$ except for *G. douglasiana* Bong. ($n = 13$) and *G. prostrata* Haenke ($n = 16$–18, 18). *Gentiana douglasiana* probably does not belong in sect. CHONDROPHYLLAE. It is unique among *Gentiana* species in its lack of an intracalycine membrane and in its pollen grains, which according to Nilsson (1967) have three colpoid apertures without ora in addition to the three oriferous colpi typical in the family.

The taxonomy of the New World CHONDROPHYLLAE is somewhat confused. The common alpine and arctic species of western North America is usually considered to be conspecific with *Gentiana prostrata* Haenke of the eastern Alps. Kusnezow (1894) referred the annual Andean *Gentiana* (as subg. EUGENTIANA) to this same species, but he also recognized *G. sedifolia*, which he considered to be a biennial, as the only other representative of the genus in South America. Gilg (1906) referred all of the Andean *Gentiana* to *G. prostrata*, but later (1916) changed his mind. Pringle (*in litt.*) considers at least three taxa of *Gentiana* to be present in the Andes: *G. sedifolia* in Venezuela, Colombia, Ecuador, and northern Peru; an unnamed taxon in the central Andes of Peru; and a plant which may be conspecific with *G. prostrata*, from central Chile south to Tierra del Fuego.

One of the two reported chromosome counts for "*Gentiana prostrata*" was made from material collected in Peru ($n = 18$, Diers, 1961). The report here of a different number for *G. sedifolia* ($n = 20$) lends support to the contention that there are at least two species of *Gentiana* in the Andes.

Gentianella Moench

The genus *Gentianella*, comprising perhaps 250 to 300 species, is nearly cosmopolitan in its distribution, but the center of diversity is in the Andes, a region from which Gilg (1916) recognized 182 species. The genus has never been monographed in its entirety, and the existing sectional classification is a residual one from Kusnezow's treatment (in Gilg, 1895) of what he called *Gentiana* subg. GENTIANELLA, several of his sections having since been elevated to generic status. Including those in this paper, chromosome numbers have now been reported for about 30 species in three sections: sect. GENTIANELLA, sect. ANDICOLA (Griseb.) Holub, and sect. ARCTOPHILA (Griseb.) Holub. All species have $n = 18$ chromosomes, with the exception of the following three: *G. moorcroftiana* (Wall. ex Griseb.) Airy Shaw, with $n = 9$ (Mehra & Vasudevan, 1972) and $2n = 26$ (Wada, 1966); *G. auriculata* (Pall.) Gillett, with $n = 24$ (Soko-

lovskaya, 1968); and *G. uliginosa* (Willd.) Börner, with n = ca. 27 (Holmen, in Löve & Löve, 1961).

Therefore, *Gentianella* in the strict sense appears to be quite homogeneous in regard to chromosome number, apparently with a base number of $x = 9$ (except for *G. auriculata* and, if the study material for Wada's report was correctly identified, for *G. moorcroftiana*), strengthening the argument for the separation of *Comastoma* (Wettst.) Toyokuni ($x = 5$) and *Gentianopsis* Ma ($x = 11, 13$) as distinct.

Although *Gentianella* and *Gentiana* L. are widely recognized as generically distinct, many specific transferals remain to be made. We propose the following new combinations relevant to this study:

Gentianella corymbosa (HBK.) Weaver & Rüdenberg, comb. nov. BASIONYM: *Gentiana corymbosa* HBK. Nov. Gen. & Sp. 3: 133 (*folio ed.*); 171 (*quarto ed.*). 1818.

Gentianella dacrydioides (Gilg) Weaver & Rüdenberg, comb. nov. BASIONYM: *Gentiana dacrydioides* Gilg, Engl. Bot. Jahrb. 22: 311. 1896.

Gentianella nevadensis (Gilg) Weaver & Rüdenberg, comb. nov. BASIONYM: *Gentiana nevadensis* Gilg, *loc. cit.* 313.

Halenia Borkh.

Most of the 70 to 80 species of *Halenia* are high-elevation plants of Central and South America. Two species are native to the Old World. Previously, chromosome numbers have been reported for eight species, representing both Old World and New World plants, and all are $n = 11$. The six species reported here all have that same number. In addition, a Costa Rican collection (*Weaver 2734*) tentatively identified as *H. rhyacophila* Allen, also $n = 11$, may represent an undescribed species.

Our observations of one bud of *Halenia inaequalis* (*Weaver 2624*) showed inversion bridges with or without fragments at Anaphase I. However, buds from another plant had cells based on $n = 11$ without irregularities. In addition, 11 bivalents plus two single, small chromosomes were observed at Metaphase II in a bud of *H. brevicornis* (*Weaver 2600*). The two single chromosomes did not pair, one of them lying free in the cytoplasm and the other located in close proximity to the end of one bivalent. Unfortunately, the material was so scarce that this collection contained only one bud with pollen-mother-cells at a countable stage. Another collection of this species (*Weaver 2625*) lacked these small chromosomes.

Lagenanthus Gilg

The sole species of this genus, the magnificent *Lagenanthus princeps* (Lindl.) Gilg, is restricted in distribution to the mountains of a small area in southwestern Venezuela and adjacent Colombia. Ewan (1952) de-

scribed a second species, *L. parviflorus*, from Panama. The type (and only specimen) (*Allen 3601*, MO), which has been examined, consists merely of a vegetative scrap and a detached flower lacking the gynoecium. Nevertheless, it is clear that this plant is not a member of the Gentianaceae.

Our collection of *Lagenanthus princeps* produced only a few cells at all suitable for study, and none of these were sufficiently clear to make an absolutely certain chromosome count. However, the haploid number appears to be $n = 40$. This number would coincide well with the results obtained from the only other supposed close relatives of *Lagenanthus* investigated to date, all of which have chromosome numbers based on $x = 10$: *Calolisianthus frigidus* ($n = 40$), *Symbolanthus* (2 species, $n = 40$), and *Chelonanthus* (3 species, $n = 20$).

Macrocarpaea (Griseb.) Gilg

A genus of perhaps 50 species, many of which are represented in collections but not yet described, *Macrocarpaea* is distributed primarily in the higher elevations of tropical South America, with outliers in Costa Rica, Panama, and the Greater Antilles. Chromosome numbers have now been reported for four species: the Jamaican *M. thamnoides* (Griseb.) Gilg (Weaver, 1969), the Costa Rican *M. valerii* Standl. (Weaver, 1972), and the two Colombian species reported here. All have $n = 21$. In addition, two collections representing undescribed Colombian species (*Weaver 2634, 2050*) have this same number of chromosomes. However, considering the large number of species and their diversity, it would be premature to expect that $n = 21$ is general in the genus.

TABLE 1. **Chromosome numbers of Gentianaceae determined during this study.**

TAXON	HAPLOID NUMBER	LOCALITY
Bartonia verna (Michx.) Muhl.	$n = 22$	UNITED STATES. North Carolina: Brunswick Co., 10 mi. NNE of Supply, *Weaver 1961* (DUKE).
Calolisianthus frigidus (Sw.) Gilg	$n = 40$	ST. VINCENT: Soufrière, *Howard, Cooley, & Weaver 17712* (A).
Chelonanthus bifidus (HBK.) Gilg	$n = 20$	COLOMBIA. Meta: ca. 5 km. N of Villavicencio, *Weaver 2640* (A).
Chelonanthus uliginosus (Griseb.) Gilg	$n = 20$	COLOMBIA. Cundinamarca: between Bogotá & Villavicencio, *Weaver 2639* (A).
Chironia baccifera L.	$n = 34$	CULTIVATED: greenhouses of the Arnold Arboretum, Jamaica Plain, Mass., U.S.A.; seeds received from the National Botanical Garden,

		Kirstenbosch, South Africa, *Weaver 2737* (AAH).
Coutoubea spicata Aubl.	$n = 15$	BRITISH HONDURAS: just W of Hattieville on the Western Highway, *Weaver 2735* (A).
Gentiana sedifolia HBK.	$n = 20$	VENEZUELA. Mérida: Laguna Mucubají, *Weaver 2620* (A).
Gentianella corymbosa (HBK.) Weaver & Rüdenberg	$n = 18$	COLOMBIA. Cundinamarca: Monserrate, *Weaver 2631* (A).
Gentianella crassulifolia (Griseb.) Fabris	$n = 18$	COLOMBIA. Nariño: Vólcan de Galeras, *Weaver 2656* (A).
Gentianella dacrydioides (Gilg) Weaver & Rüdenberg	$n = 18$	COLOMBIA. Putumayo: between El Encano & Santiago, *Weaver 2655* (A).
Gentianella nevadensis (Gilg) Weaver & Rüdenberg	$n = 18$	VENEZUELA. Mérida: Laguna Mucubají, *Weaver 2606* (A).
Halenia brevicornis (HBK.) G. Don	$n = 11 + 2$	VENEZUELA. Mérida: Cuenca Santo Domingo, *Weaver 2600* (A).
	$n = 11$	VENEZUELA. Mérida: Teleferico de Mérida, between La Aguada & La Montaña, *Weaver 2625* (A).
Halenia cuatrecasasii Allen	$n = 11$	COLOMBIA. Cundinamarca: Monserrate, *Weaver 2630* (A).
Halenia phyllophora Allen	$n = 11$	COLOMBIA. Putumayo: between El Encano & Santiago, *Weaver 2654* (A).
Halenia rhyacophila Allen	$n = 11$	COSTA RICA. Cartago: Cerro Buenavista, *Weaver 2733* (A).
Halenia viridis (Griseb.) Gilg	$n = 11$	VENEZUELA. Mérida: Laguna Mucubají, *Weaver 2605* (A).
Halenia inaequalis Wedd.	$n = 11$	VENEZUELA. Mérida: Teleferico de Mérida, between La Aguada & La Montaña, *Weaver 2624* (A).
Lagenanthus princeps (Lindl.) Gilg	$n =$ ca. 40	VENEZUELA. Tachira: base of Paramo de Tamá, *Weaver 2612* (A).
Macrocarpaea densiflora (Benth.) Ewan	$n = 21$	COLOMBIA. Tolima: between Fresno & Manizales, *Weaver 2644* (A).
Macrocarpaea glabra (L. f.) Gilg	$n = 21$	COLOMBIA. Cundinamarca: above Bogotá on road to Villavicencio, *Weaver 2636* (A).
Symbolanthus tricolor Gilg	$n = 40$	COLOMBIA. Cundinamarca: near San Miguel, *Weaver 2635* (A).

ACKNOWLEDGMENTS

We wish to acknowledge a most generous grant from the Atkins Fund, which made most of the field work possible. We are grateful also to Dr. James Pringle of the Royal Botanical Gardens, Hamilton, Ontario, Canada, for making available his unpublished observations on *Gentiana* in South America.

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APPENDIX. Previously reported chromosome numbers in the genera of Gentianaceae investigated during this study.

TAXON	HAPLOID NUMBER	REFERENCE
Bartonia Muhl.		
Bartonia paniculata (Michx.) Muhl.	26	Rork, 1949
Bartonia virginica (L.) BSP.	26	Rork, 1949
	ca. 26	Moore, in Gillett, 1959
Chelonanthus (Griseb.) Gilg		
Chelonanthus alatus (Aubl.) Pulle	20	Weaver, 1969
Gentiana L.		
Sect. CHONDROPHYLLAE Bunge		
Gentiana altaica Laxm.	13	Sokolovskaya & Strelkova, 1938
Gentiana argentea Royle	10	Mehra & Vasudevan, 1972
Gentiana carinata Griseb.	10	Mehra & Gill, 1968
Gentiana capitata Ham.	10	Mehra & Vasudevan, 1972
Gentiana crutwellii H. Sm.	10	Borgmann, 1964
Gentiana douglasiana Bong.	13	Taylor & Mulligan, 1968
Gentiana ettinghausenii F. Muell.	10	Borgmann, 1964
Gentiana piundensis Van Royen	10	Borgmann, 1964
Gentiana prostrata Haenke	18	Diers, 1961
	16–18	Johnson & Packer, 1968
Gentiana pyrenaica L.	13	Küpfer & Favarger, 1967
	13	Favarger & Küpfer, 1968
Gentiana zollingeri Fawcett	10	Wada, 1956
	10	Wada, 1966
Gentianella Moench		
Sect. GENTIANELLA		
Gentianella acuta (Michx.) Hiit.	18	A. Löve, 1954
Gentianella amarella (L.) Börner	18	D. Löve, 1953
subsp. *lingulata* (Ag.) Löve & Löve	18	A. & D. Löve, 1956
Gentianella anisodonta (Borbás) Löve & Löve	18	Favarger, 1965
Gentianella aspera (Hegetschw. & Heer) Dorstál ex Skalický, Chrtek, & Gill	18	Favarger, 1965
Gentianella auriculata (Pall.) J. M. Gillett	24	Sokolovskaya, 1968
Gentianella austriaca (A. & J. Kern.) Holub	18	Favarger, 1952
Gentianella campestris (L.) Börner		
subsp. *campestris*	18	Favarger, 1949

subsp. *islandica* (Murb.) Dörfler	18	A. & D. Löve, 1956
Gentianella engadinensis (Wettst.) Holub	18	Favarger, 1965
Gentianella germanica (Willd.) Warburg	18	Reese, in A. & D. Löve, 1961
Gentianella hypericifolia (Murb.) Pritchard	18	Küpfer & Favarger, 1967
	18	Favarger & Küpfer, 1968
Gentianella insubrica (H. Kunz) Holub	18	Favarger, 1952
Gentianella moorcroftiana (Wall. ex Griseb.) Airy Shaw	9	Mehra & Vasudevan, 1972
	13	Wada, 1966
Gentianella rhaetica (A. & J. Kern) A. & D. Löve	18	Favarger, 1965
Gentianella uliginosa (Willd.) Börner	ca. 27	Holmen, in A. & D. Löve, 1961
Sect. ANDICOLA (Griseb.) Holub		
Gentiana aff. *briquetiana* Gilg *	18	Diers, 1961
Gentiana aff. *brunneo-tincta* Gilg *	18	Huynh, 1965
Gentiana aff. *dolichopoda* Gilg *	18	Diers, 1961
Gentiana inaequicalyx Gilg *	18	Diers, 1961
Gentiana aff. *kuntzei* Gilg *	18	Diers, 1961
Gentianella peruviana (Griseb.) Fabris	18	Diers, 1961
Gentiana primuloides Gilg *	18	Diers, 1961
Gentiana pulla Fabris *	18	Diers, 1961
Gentianella punicea (Wedd.) Holub	18	Diers, 1961
Gentianella saxosa (G. Forst.) Holub	18	Favarger, 1952
Gentianella umbellata (R. & P.) Favarger	18	Huynh, 1965
Sect. ARCTOPHILA (Griseb.) Holub		
Gentianella aurea (L.) H. Sm.	18	D. Löve, 1953
Gentianella quinquefolia (L.) Small	18	Rork, 1949
Halenia Borkh.		
Halenia crassiuscula Robins. & Seat.	11	Beaman, *et al.*, 1962
Halenia corniculata (L.) Cornaz	11	Sokolovskaya, 1963
	11	Wada, 1966
Halenia decumbens Benth.	11	Niehaus & Wong, Jr., 1971

Halenia deflexa (Sm.) Griseb.	11	Mulligan, 1967
Halenia elliptica D. Don	11	Favarger, 1952
Halenia multiflora Benth.	11	Niehaus & Wong, Jr., 1971
Halenia shannonii Briq.	11	Beaman, *et al.*, 1962
Halenia umbellata (R. & P.) Gilg	11	Favarger & Huynh, 1965
	11	Huynh, 1965
Macrocarpaea (Griseb.) Gilg		
Macrocarpaea thamnoides (Griseb.) Gilg	21	Weaver, 1969
Macrocarpaea valerii Standl.	21	Weaver, 1972
Symbolanthus G. Don		
Symbolanthus pulcherrimus Gilg	40	Weaver, 1969

* Combination in *Gentianella* not yet made.

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